

THE SILURIAN TRILOBITE *ENCRINURUS PUNCTATUS* (WAHLENBERG) AND ALLIED SPECIES

by R. P. TRIPP

ABSTRACT. The lectotype pygidium of *Encrinurus punctatus* (Wahlenberg), the type species, is from the Wenlock Series of the Island of Gotland, in which two allied species of *Encrinurus* are present; pygidia are not diagnostic but the size of the lectotype indicates that it should be attributed to the species with larger-sized individuals. An *E. punctatus* species-group is defined; conformity with the basic arrangement of tubercles on cranium and pygidium is a necessary, but not sufficient, criterion of inclusion. The group includes also the following species: *E. macrourus* Schmidt, the smaller species from Gotland; *E. tuberculatus* (Buckland), a name revived for the British Wenlock form commonly referred to *E. punctatus*; *E. stubblefieldi* sp. nov. from the Ludlow Series of Shropshire; *E. onniensis* Whittard from the Upper Llandovery of Shropshire, and *E. deomenos* sp. nov. from the Jupiter Formation of Anticosti Island.

THE terminology used is unaltered from that of my earlier paper (1957, p. 60) except that the term fossula is used for the anterior pit in the longitudinal furrow. Hamada (1959, p. 83) considers the area between the preglabellar furrow and the facial sutures to be a true preglabellar field, but as Temple (1956, p. 424) points out 'a true preglabellar field does not bear the axial part of the facial suture and is not typically separated by furrows from the cheeks'. I agree with Temple in considering this area homologous with part of the anterior border of the cranium in other members of the Cheiruracea.

Previous research. *Entomostracites punctatus* Wahlenberg 1821 has been established as the type species of the genus *Encrinurus* Emrich (1844, p. 16), and the pygidium from the Island of Gotland which Wahlenberg figured has been selected as lectotype (Opinion 537 of the International Commission on Zoological Nomenclature). Rosenstein (1941) has published an excellent account of the Estonian form of the species, but unfortunately her paper is not widely available; she recognized the regularity of arrangement of certain cranial tubercles, and demonstrated that there is a correlation between the positions of the axial and pleural tubercles on the pygidium.

Definition of the E. punctatus species-group. Glabella widening markedly forward. Basal lateral lobes almost obsolete, middle and anterior lateral lobes represented by nodular tubercles; similar lateral tubercles on frontal lobe and false preglabellar field. Pairs of large tubercles placed opposite middle and anterior lateral lobes; two or three main rows on frontal lobe. False preglabellar field ill defined, bearing a single row of large tubercles. Fixigenal spines well developed. A column of median, or occasionally submedian, tubercles on axis of pygidium; typically eight pairs of pleurae each with a tubercle.

The following species are here referred to the group: *E. macrourus* Schmidt, *E. tuberculatus* (Buckland), *E. stubblefieldi* sp. nov., *E. onniensis* Whittard, *E. deomenos* sp. nov. None of the specimens from Scotland attributed to *E. punctatus* fall within the group. No specimens from the mainland of North America have been studied.

System of notation applied to glabellar tubercles. In the present work the system of notation applied to glabellar tubercles by the author in 1957 is adopted (text-fig. 1). The transverse rows of tubercles are numbered I to VI starting from the back; tubercles which occur between the transverse rows are symbolized by the small roman numeral of the row in front; pairs of tubercles are numbered in arabic numerals distally from the centre line. One refinement is necessary: many Silurian species have two tubercles placed one behind the other, between the proximal and lateral tubercles in row III; these tubercles, which may occur singly, are distinguished as III-2* and III-2*. Similarly, the two median tubercles sometimes present between rows III and IV are indicated as iv-0*. The four tubercles in row II are the most consistent in occurrence, but even these are not invariably present (Pl. 66, fig. 8), and adventitious tubercles sometimes occur between them (Pl. 65, fig. 7). Tubercles which occur on over 90 per cent. of the specimens are regarded as regular, while those on 10 per cent.–90 per cent. are recorded in parentheses in the tubercle formula. The regularity of arrangement of the tubercles on the frontal lobe becomes obscured in heavily tuberculated specimens. The presence or absence of tubercles is not dependent on size of individual (text-fig. 2); for example, tubercles iii-0 and III-2 are present on even the smallest British specimens but lacking on some of the larger specimens.

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SYSTEMATIC DESCRIPTIONS

Encrinurus punctatus (Wahlenberg)

Plate 65, figs. 9–11, 13–14; Plate 66, figs. 2–3; Plate 67, figs. 5–8; Plate 68, figs. 7, 8, 10

Entomostracites punctatus Wahlenberg 1821, p. 32, pl. 2, fig. 1* (*non* fig. 1).

Encrinurus punctatus Emmrich 1844, p. 16.

Encrinurus punctatus Nieszkowski 1857, p. 604, pl. 3, figs. 6, 7.

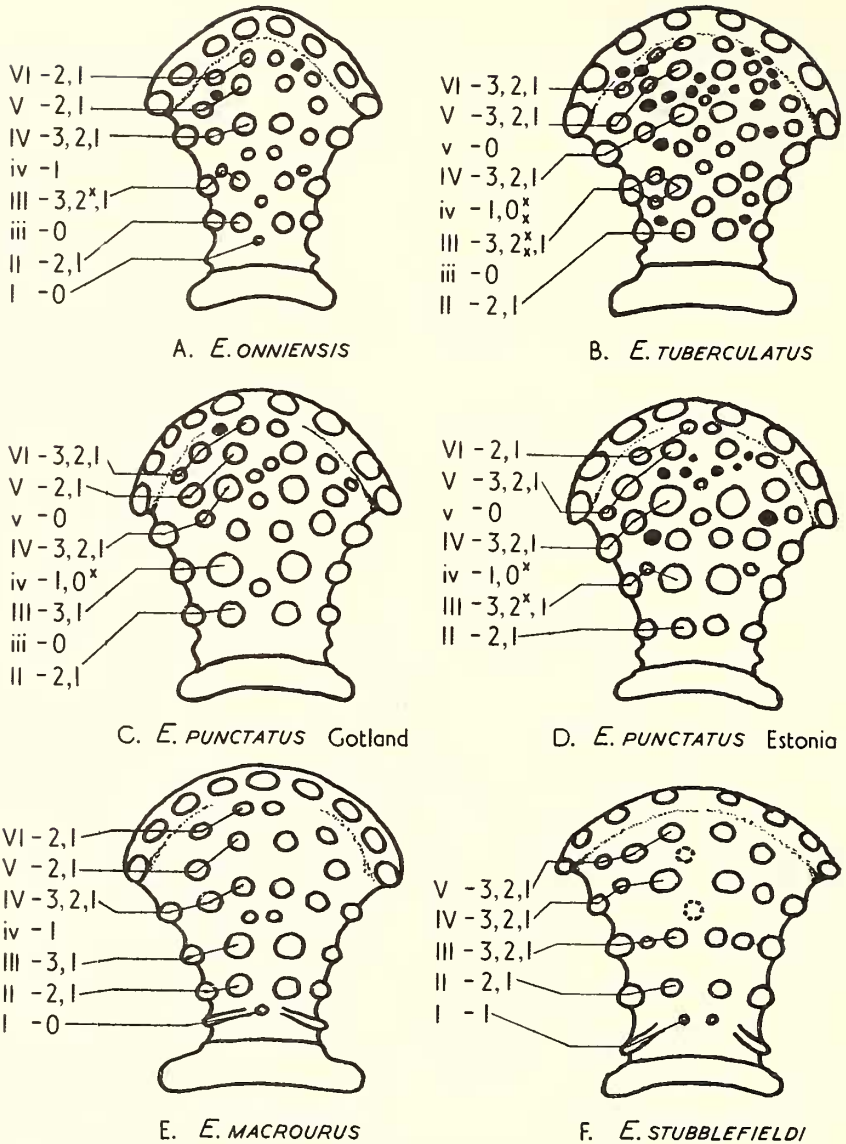
Encrinurus punctatus Schmidt 1881, p. 225, pl. 14, figs. 11–13, pl. 15, fig. 18.

Encrinurus punctatus Lindström 1901, p. 56, pl. 4, figs. 4–9, 12, 13.

Encrinurus punctatus Öpik 1937, p. 118, pl. 25, fig. 5.

Encrinurus punctatus Rosenstein 1941, p. 49, pl. 1, figs. 1–11; pl. 2, figs. 1–3, 5, *non* 4–4b; pl. 3, figs. 1–10.

Diagnosis. Glabella strongly convex, standing well above cheeks; cheeks narrow.



TEXT-FIG. 1. Arrangement of glabellar tubercles in certain species of the *E. punctatus* group. A, *E. onniensis* Whittard, Shropshire, after the syntype OUM C1 (Pl. 65, fig. 16). B, *E. tuberculatus* (Buckland), Worcestershire, after BM In. 48007 (Pl. 65, fig. 7). C, *E. punctatus* (Wahlenberg), Gotland, after RS Ar. 20320 (Pl. 65, fig. 9). D, *E. punctatus* (Wahlenberg), Estonia, after PIT Tr 1921 (Pl. 65, fig. 14). E, *E. macrourus* Schmidt, Gotland, after RS Ar. 30445 (Pl. 65, fig. 4). F, *E. stubblefieldi* s. nov., Shropshire, after GSM 36846 (Pl. 65, fig. 12). Tubercles regarded as adventitious are shaded.

Axial furrows deep and narrow. False preglabellar field rarely with a median tubercle. Central body of hypostome strongly convex anteriorly, with median lobe not projecting beyond anterior border.

Lectotype. PIU 1200 (pygidium figured Wahlenberg 1821, pl. 2, fig. 1*). Selected and figured by Tripp and Whittard 1956, p. 259, pl. 3, figs. 1, 2. Gotland.

Dimensions:

Length of pygidium (excluding articulating half-ring) 13·6 mm.

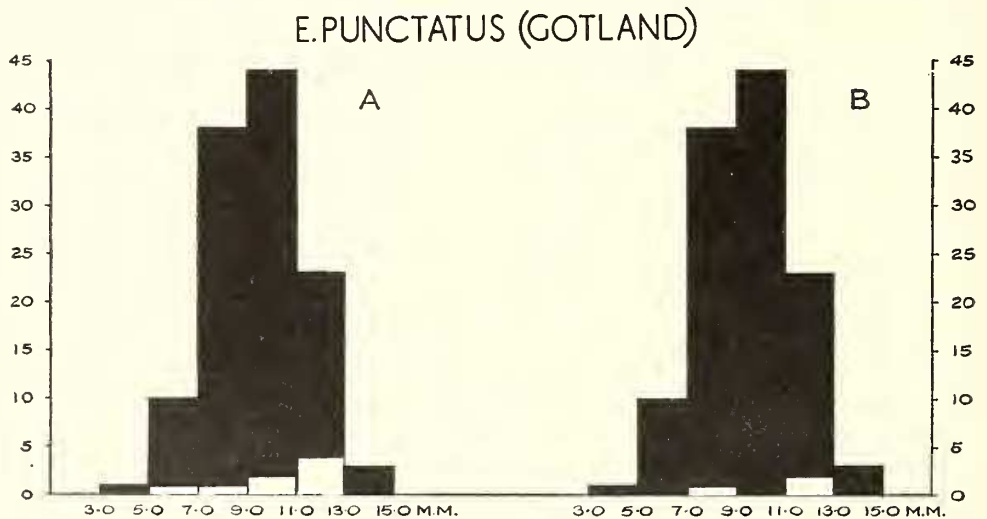
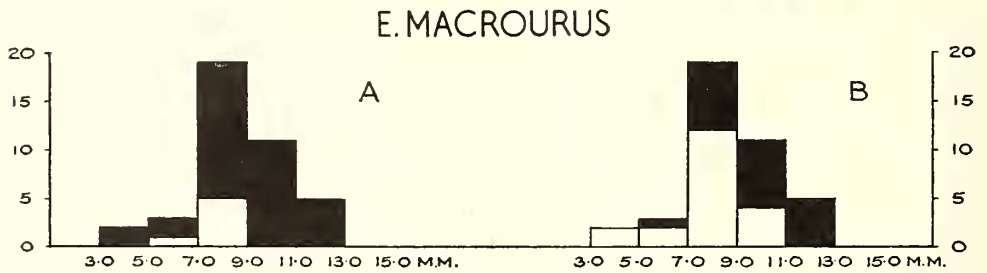
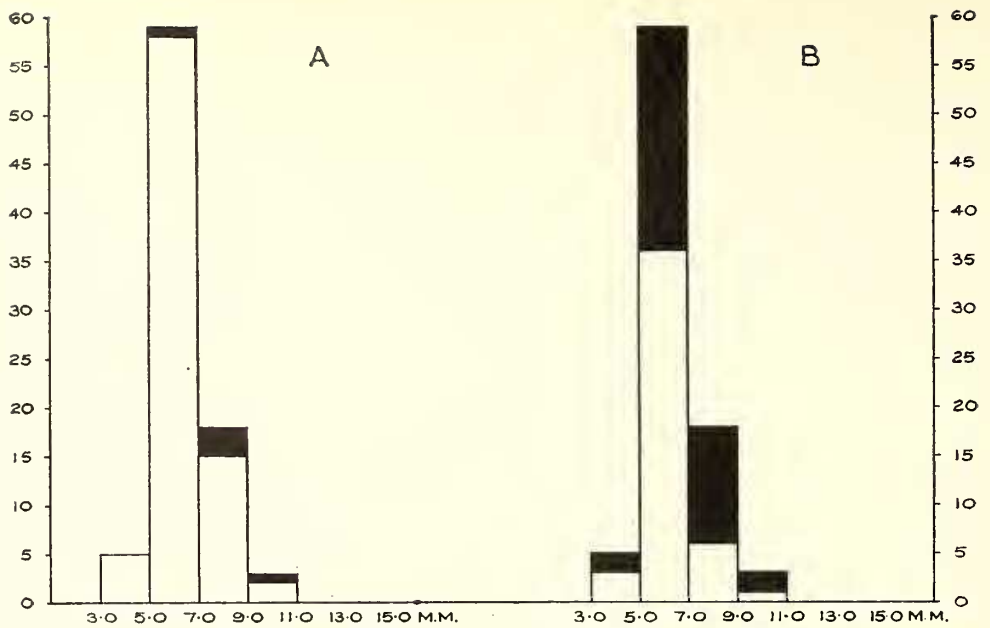
Width of pygidium 14·5 mm.

Width of axis at front 4·5 mm.

Occurrence. In Gotland as follows: Upper Visby Marl (Upper Llandoverly), Visby. Högklint Group (Wenlockian), Visby; Lansä, Fårö. Slite Group (Wenlockian), Barabacke; Biskops; Eskelhem; Fardume; Follingbo; Klintsvärn; Lergravsviken; Medebys; Myrsjö; Omkr; Slite; Stave; Stormyr; Tjelders; Tofta; Underifrån; Utbunge; Västerhejde; Västergarn; Wallstena. In Estonia as follows: Jaani Marl (J₁), Island of Saaremaa. In Norway as follows: Stage 8d (*Monograptus riccartonensis* Zone), Malmøya.

Description. Cephalon elliptical in outline, strongly convex. Glabella strongly rounded in outline anteriorly, narrowing steadily and strongly backwards to about two-thirds its anterior width; moderately convex longitudinally, strongly convex transversely. Glabella rises well above cheeks at back. Basal glabellar lobe consists of low lateral ridges and an occasional small median tubercle. Middle and anterior lateral lobes represented by nodular tubercles; similar lateral tubercles occur on frontal lobe and on false preglabellar field. These four pairs of tubercles overhang axial furrows. Middle and anterior furrows mere depressions between tubercles. Frontal lobe long. False preglabellar field continuous with glabella in convexity; preglabellar furrow broad and shallow laterally, dying out mesially. Occipital ring moderately arched transversely, considerably broader than posterior part of glabella, somewhat flattened longitudinally; occipital furrow shallow, bowed gently forwards mesially. Axial furrows deep and narrow, deepening abruptly opposite preglabellar furrow and continuing at full depth on to free cheeks; small fossulae at about own diameter behind facial sutures. Apodemes near extremities of lateral glabellar and occipital furrows, immediately inside junctions with axial furrows; occipital pair transversely elongate, basal pair a short distance in front; middle and anterior pairs smaller. A pair of small pits in corresponding positions in preglabellar furrow. Tubercles are usually hemispherical, and sometimes granular; tubercles usually perforate; a single perforation at summit of glabellar tubercles, several perforations may be present on other tubercles. Glabellar tubercle formula: (1-0); II-1, 2; (iii-0); III-1, (2*), 3; iv-(0*), 1; IV-1, 2, 3; v-(0); V-1, 2, (3); VI-1, (2, 3). Tubercle 1-0 is small, placed close behind row II. Eight, nine (never with one central), or ten tubercles on false preglabellar field; small additional tubercles occasionally present.

Fixed cheeks strongly convex, sloping steeply outwards. Palpebral lobes lingulate, almost vertical, rising higher than glabella, situated close to glabella, mid-length opposite middle lateral furrows; palpebral furrows broad and shallow. Posterior borders short (sag.) and transverse proximally, expanding steadily beyond mid-width and curving backwards; a small articulating ledge at back. Posterior border furrows broadest near



TEXT-FIG. 2. Histograms illustrating occurrence of certain tubercles in *E. tuberculatus*, *E. punctatus*, and *E. macrourus*.

Ordinate—number of specimens. A, shaded—with tubercle iii-0; A, unshaded—without tubercle iii-0. B, shaded—with any of the four III-2* tubercles; B, unshaded—without any of the four III-2* tubercles.

Abcissa—length of cranium in mm.

mid-width of cheeks. Lateral borders moderately wide, uniting with posterior borders to form slender fixigenal spines, which are directed backwards and slightly outwards and extend to the fifth thoracic segment. Doublure narrow, widening at genal angles. Anterior branches of facial sutures curve forwards and inwards, crossing axial furrows and separating false prelabellar field from pseudoglabellar areas of free cheeks; posterior branches curve outwards and backwards, crossing lateral borders opposite occipital furrow. Fixed cheeks tuberculate and shallowly pitted (particularly laterally); a column of four large tubercles overhanging axial furrow. Base of palpebral lobe faintly tuberculate. Posterior borders usually smooth, occasionally with a row of low tubercles; a few tubercles near bases of fixigenal spines.

Eyes pedunculate, large, visual surface occupies upper half of lobe. Free cheeks large, sloping almost vertically downwards. Pseudoglabellar areas moderately long (exs.) and gently convex. Axial furrows deep, continuous with border furrows. Borders widen gradually forward to axial furrows, and narrow out rapidly in front of pseudoglabellar areas. Lateral border furrows broad and shallow. Broad depressions run inwards and forwards from axial furrows, separating pseudoglabellar areas from borders. Doublure convex, narrowing forwards and backwards from axial furrows, equal to border in width and sharply upturned proximally. Shallow lateral vincular grooves for accommodation of extremities of posterior thoracic segments when enrolled extend back from mid-length of cheeks. Inner areas of cheeks shallowly pitted, with an irregular arc of four or five tubercles near eyes and one or more tubercles laterally. Tubercles scattered two-deep on pseudoglabellar areas. Lateral borders with a main row of seven tubercles increasing in size forwards, and a smaller, less regular, outer row. Borders and border tubercles more coarsely granular than rest of cephalon.

Rostral plate cuneiform, but very variable in shape, narrow, held in an almost vertical position between free cheeks, projecting downwards together with adjacent parts of free cheeks; truncated by rostral suture, occasionally bearing small tubercle; swollen and granular forwards, inturned and narrowing out between doublures of free cheeks at forefront.

Hypostome diamond-shaped, four-fifths as wide as long, broadly rounded anteriorly. Central body oval, three-quarters length of hypostome, moderately convex in both directions; longitudinal median lobe projecting and reaching to anterior border, widening slightly and fading out towards back. Maculae strongly swollen, smooth. Anterior border short (exs.), thickened and flexed ventrally downwards at median lobe; border furrow broad laterally, narrowing mesially. Anterior wings large, sloping obliquely upwards, backwards, and outwards, truncate laterally; a rounded wing process near margin. Postero-lateral extensions of wings strongly upturned. Lateral borders narrow, subparallel for a short distance, converging and increasing steadily in width posteriorly, produced into an ogive-shaped tongue. Lateral doublure widens anteriorly to form posterior wings, and posteriorly beneath tongue. Surface of central body and tongue finely granular.

Thorax about one and a third times length of cephalon, composed of eleven segments. Axis one-third anterior width of thorax, gently arched transversely, narrowing comparatively little towards back. Axial rings weakly convex from front to back, bowed forwards mesially, with faint lateral nodes. Articulating half-rings and furrows strongly developed; stout apodemes near extremities of articulating furrows. Indications of a

broken spine, or a tubercle, on tenth ring. Axial furrows shallow and narrow. Pleurae straight and horizontal to mid-width, directed more or less strongly backwards and downwards laterally. Posterior pleurae bent more strongly downwards and less strongly backwards at fulcrum, which is placed nearer axis. Inner parts of pleurae composed of a broad, gently convex, posterior band, separated by a sharp furrow from a narrow (exs.), depressed anterior band; a ledge at back of posterior band narrows out before fulcrum, and serves to articulate with anterior band of adjacent segment along a slightly sinuous suture line. Laterally, posterior band broadens, pleural furrow narrows, and bevelled articulating facets develop between band and furrow, anterior band forming a narrow border. Lateral margins of posterior bands rounded, lateral margins of articulating facets oblique. (Appearance of internal moulds differs considerably from that of testate specimens in that pleural furrows and ledges are broader, due to differential thickness of shell.) A low tubercle usually placed near fulcrum, successive pleurae sometimes with tubercles placed alternately nearer and farther from axis; additional tubercles sometimes occur.

Pygidium excluding mucro longer than cephalon, triangular, approximately as long as wide. Axis weakly arched transversely, narrowing steadily backwards, ill defined posteriorly. First ring the most strongly developed, confluent with first pair of pleurae on external, but not on internal, surface; first ring furrow continuous, but shallower mesially than laterally. Subsequent ring furrows more or less discontinuous mesially, becoming successively shorter and fainter towards back, hindmost obscure; between twenty and thirty rings can usually be counted. Articulating half-ring and furrow almost as long as first ring. Axial furrows moderately deep posterior to first pleurae, dying out posteriorly. Pleural lobes comparatively wide and moderately convex, sloping downwards with variable steepness, which increases towards back. Eight pairs of raised ribs which widen slightly laterally; ribs broad and flattened on external surface, narrow on internal moulds. First seven pairs of ribs terminate bluntly on lateral margins, eighth die out just beyond apex of axis. Interpleural furrows deep and moderately broad proximally, becoming shallower and narrower laterally; seventh pair do not reach lateral margins. Comparative width of ribs and furrows not consistent between specimens. Mucro of moderate length sometimes developed. Anterior half-pleurae short (exs.), marked off by sharp furrows. Bevelled articulating facets develop laterally between half-pleurae and first ribs, as on thoracic segments. Doublure widens towards back; inner margins converge less strongly in posterior one-fourth of their length and meet at an acute angle opposite apex of axis. Doublure granular; a row of five or more perforations pierce test horizontally at extremities of pleurae and along mucro (Rosenstein 1941, pl. 2, fig. 5). Axis of pygidium bears a row of six or seven median tubercles, spaced out at backwardly decreasing intervals. Pleurae bear a tubercle either close to axial furrow, or placed laterally, occasionally in both or intermediate positions. Size of pleural tubercles varies greatly between specimens. Smallest pygidium (2.3 mm. in length) has a short slender mucro; only seven pairs of pleurae present.

Remarks. Dr. J. Ernhold Hede has kindly studied the lectotype pygidium. He states that it is from beds which are certainly younger than the Upper Visby Marl and older than the Klinteberg Group; that its age is without doubt Wenlockian, and that it is most probably from the Höglint Group (for stratigraphical table see Hede 1960, pp. 47-52).

Two species of *Encrinurus* of the *punctatus* type occur in the Wenlock Series of Gotland, and unfortunately the pygidia cannot be distinguished morphologically. The most common is a comparatively large form, with 2σ limits for length of cranidium of 4.8–12.5 mm., compared with 4.0–8.4 mm. for the smaller species. The lectotype is a large non-mucronate pygidium measuring 13.6 mm. in length; comparison with entire specimens shows that the length of the cranidium is 15–20 per cent. less than that of the pygidium, indicating a cranial length of 10.8–11.6 mm. for the type.

It is reasonably certain, therefore, that the type pygidium is conspecific with the larger cranidia. Such morphological evidence as is available—the greater convexity for instance—supports this view. The smaller form is referred to *E. macrourus* (see below), a species which becomes common in the Ludlow series.

Specimens of *E. punctatus* from the Höglint Group, the Slite Group and Estonia differ in size and there are considerable variations in the arrangement of glabellar and preglabellar tubercles (see Table 1). The posterior tongue of the hypostome from Estonia, figured Pl. 67, fig. 5, is short, though slightly abraded.

Encrinurus tuberculatus (Buckland)

Plate 65, figs. 5–8; Plate 66, figs. 4–11; Plate 67, figs. 9–10; Plate 68, figs. 4–6

Calymène variolaire Brongniart 1822, pl. 1, fig. 3a (non fig. 3b).

Asaphus tuberculatus Buckland 1836, vol. 2, p. 74, pl. 46, fig. 6. (= pl. 1 fig. 3a in Brongniart 1822).

Cybele punctata Fletcher 1850, p. 158, pl. 32, figs. 1–5.

Encrinurus punctatus Salter 1853, p. 6, pl. 4, figs. 15, 16 (non fig. 14).

Diagnosis. Glabella strongly convex, standing well above cheeks. Axial furrows deep and narrow. Glabella strongly tuberculate. Rostral plate protuberant. Central body of hypostome weakly convex anteriorly with median lobe ‘waisted’, not projecting beyond anterior border.

Holotype. Specimen figured by Buckland 1836, pl. 46, fig. 6 (dorsal shield). Present whereabouts unknown. Wenlock Limestone, Dudley, Worcestershire.

Occurrence. In Britain as follows: Woolhope Limestone, Malvern Tunnel, Worcestershire. Wenlock Limestone and Shale, Dudley, Worcestershire; Much Wenlock, Shropshire; Colwall and Malvern, Herefordshire; Walsall, Staffordshire; Pen-y-lan, near Cardiff, Glamorgan.

Description. Cheeks broader compared with glabella than in type form. Glabellar tubercle formula (I-0); II-1, 2; iii-0; III-1, 2*, 3; iv-0*, 1; IV-1, 2, 3; v-0; V-VI-1, 2, 3. Adventitious tubercles commonly occur particularly on the frontal lobe. Typically with eight tubercles on false preglabellar field. Eye lobes more slender and higher, and situated further forward—opposite anterior lateral glabellar lobes—and farther from glabella. A conspicuous row of tubercles at base of palpebral lobe. Pseudoglabellar areas of free cheeks longer (exs.), tubercles sometimes three-deep. Front part of the appropriately named rostral plate, together with adjacent parts of cheeks, projects forwards and downwards like a beak. Hypostome more strongly rounded in anterior outline; longitudinal convexity weak anteriorly. Median lobe not projecting beyond anterior border, more strongly arched transversely, longer and distinctly ‘waisted’ near mid-length. Anterior border of hypostome flexed more strongly mesially. Posterior tongue longer. Central

body and tongue more coarsely granular; numerous smooth, transverse depressions on central body may be areas of muscle attachment.

Axis of thorax less than one-third width of thorax anteriorly. Indications of a median broad-based axial spine almost always present on tenth thoracic ring, sometimes also on seventh, ninth, or eleventh rings. When preserved spine curves backwards and extends for about one and a half times width of ring. Mucro of pygidium usually of moderate length, sometimes upcurved, never absent.

Remarks. Buckland's explanation of his pl. 46, fig. 6 is as follows: 'Asaphus tuberculatus; a highly ornamented species from the Transition lime-stone of Dudley; in the collection of Mr. Johnson, of Bristol. The back alone is composed of flexible plates.' (Curtis.) Parts of Mr. Jas. R. Johnson's Collection are in the City Museum, Bristol, and in the British Museum (Natural History), but there is no trace of this specimen.

Many specimens of *E. tuberculatus* and *E. macrourus* are preserved with the hypostome in position. The hypostome fits exactly against the doublure of the cephalon along the sinuous hypostomal suture, the rostral plate and adjacent parts of the free cheeks

EXPLANATION OF PLATE 65

All photographs are of testate specimens unless otherwise stated. The specimens were coated with ammonium chloride before being photographed.

Figs. 1-4. *Encrinurus macrourus* Schmidt. 1, Klinteberg Group (Lower Ludlovian), Eksta, Gotland. RS Ar. 30206, $\times 4$. The median preglabellar tubercle off-centre. 2, Högklint Group (Wenlockian), Kappelshamn, Gotland. PIU, $\times 5$. The median preglabellar tubercle off-centre. 3, Klinteberg Group (Lower Ludlovian), Eksta, Gotland. RS Ar. 30673, $\times 6$. 4, Hemse Group (Lower Ludlovian), Petesviken, parish of Häblingbo, Gotland. RS Ar. 30445, $\times 6$. No inter-row tubercles present; eight preglabellar tubercles.

Figs. 5-8. *Encrinurus tuberculatus* (Buckland). 5, Wenlock Limestone, Dudley, Worcestershire. OUM C368, $\times 4$. Sparsely tuberculated specimen. 6, Wenlock Shale, Malvern, Herefordshire. GSM Z.4103, $\times 3$. A typical specimen; inter-row tubercles iv-0*, 1 present. 7, Wenlock Shale, Malvern, Herefordshire. BM In. 48007, $\times 4$. Heavily tuberculated specimen, with adventitious tubercles in row II. 8, Wenlock Limestone, Dudley, Worcestershire. GSM 36304, $\times 3\frac{1}{2}$. Five preglabellar tubercles on the right side.

Figs. 9-11. *Encrinurus punctatus* (Wahlenberg). 9, Slite Group (Wenlockian), Eskelhem, Gotland. RS Ar. 20320, $\times 3$. Five preglabellar tubercles on the left side. 10, Slite Group (Wenlockian), Follingbo, Gotland. RS Ar. 47293, $\times 4$. Heavily tuberculated specimen; probably ten preglabellar tubercles. 11, Högklint Group (Wenlockian), 'Vattenfallet' (the 'Waterfall'), Visby, Gotland. RS Ar. 30479, $\times 3$.

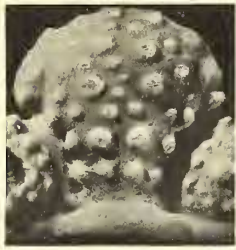
Fig. 12. *Encrinurus stubblefieldi* sp. nov., 'Upper Ludlow Shales,' Whitcliff, Shropshire, GSM 36846 (the holotype), $\times 6$. Internal mould.

Figs. 13-14. *Encrinurus punctatus* (Wahlenberg). Jaani Marl, Jaani, Saaremaa, Estonia. 13, PIT Nr 1920, tubercle iii-0 lacking. 14, PIT Tr 1882 (Bölauf Collection), $\times 3$. Exceptionally large specimen; figured by Rosenstein 1941, pl. 1, figs. 1-4.

Fig. 15. *Encrinurus* sp. Damery Beds, Woodford, near Tortworth, Gloucestershire. BM In. 54000, $\times 4$. Internal mould.

Fig. 16. *Encrinurus onniensis* Whittard. Purple Shales (Upper Valentian), Onny River Section, near Cheney Longville, Shropshire. OUM C1, $\times 4$. Internal mould.

Figs. 17-20. *Encrinurus variolaris* (Brongniart). 17, Wenlock Limestone, Dudley, Worcestershire. BU 723 (Holcroft Collection), $\times 4$. Note coalescence of a pair of tubercles in row I. 18, Wenlock Shale. Malvern, Herefordshire. OUM C372, $\times 5$. 19, Wenlock Limestone, Dudley, Worcestershire. BU 724 (Holcroft Collection), $\times 8$. 20, Wenlock Limestone, Dudley, Worcestershire. BU 725 (Holcroft Collection), $\times 4$. A median tubercle in row I.



1



2



3



4



5



6



7



8



9



10



11



12



13



14



15



16



17



18



19



20

projecting downwards in conformity with the median flexure of the anterior border of the hypostome. When held in this position the wing processes appear to be in contact with the fossulae (Pl. 67, fig. 2) and the tip of the tongue lies opposite the posterior margin of the occipital ring and comparatively close to it (Pl. 66, fig. 4b). The proximity of the projecting rostral plate to the median lobe of the hypostome would prevent any appreciable rocking action, so practically no movement can have been possible. The same condition applies in the case of *E. variolaris* (Brongniart); Temple (1954, p. 317) writes: 'The cephalon and hypostome of *E. variolaris* seem to have formed together a rigid whole, for it is unlikely that any movement could have taken place during life along the curved hypostomal suture or the facial sutures, although there may have been sufficient elasticity in the integument to allow a very small amount of bending to occur.'

Rosenstein (1941, p. 60) demonstrated that in Estonian *Encrinurus* pygidia there is a correlation between the positions of the axial and pleural tubercles; 94 per cent. of specimens with the first tubercle on the first ring have the tubercle on the second pleurae farther from axis than the others; 75 per cent. of specimens with the first tubercle on the second ring have the tubercle on the third pleurae the farthest from the axis. The percentage of specimens which demonstrate this correlation is much larger in *E. punctatus* than in *E. tuberculatus*, even when specimens which show a slight displacement, or a displacement on one side only, are included (see Table 1).

The synonymy of *E. punctatus calcareus* Salter (1853, p. 6) cannot be established at present. Woolhope is the principal, if not the only, locality mentioned by Salter, but there are no specimens from the Woolhope Inlier in the collections studied.

Encrinurus macrourus Schmidt

Plate 65, figs. 1-4; Plate 66, figs. 1a-c; Plate 67, figs. 1-4; Plate 68, figs. 1-3, 9

Encrinurus punctatus var. *macrourus* Schmidt 1859, p. 438.

Encrinurus punctatus Rosenstein 1941, pl. 2, figs. 4-4b.

Diagnosis. Glabella widening strongly towards front, weakly convex, rarely rising above cheeks at back. Axial furrows broad. Usually nine tubercles on false preglabellar field, one medial. Central body of hypostome weakly convex anteriorly, with median lobe projecting beyond anterior border.

Lectotype. PIT Tr 1905 (thorax and pygidium). Pl. III, figs. 4a, b. Hemse Group (*Lower Ludlovian*), Petesviken, parish of Hablingbo, Gotland. Selected hereby.

Dimensions:

Length of pygidium (extremity broken)	9.0 mm.
Width of pygidium	7.8 mm.
Anterior width of axis	2.9 mm.

Occurrence. In Gotland as follows: Lower Visby Marl (Upper Llandovery)?; Norderstrand. Upper Visby Marl (Upper Llandovery), Lummelunda; Visby. Högklint Group (Wenlockian), Kapelshamn; Visby. Slite Group (Wenlockian), Klintsgvarn; Slite. Mulde Marle (Wenlockian), Fröjel. Klinteberg Group (*Lower Ludlovian*), Eksta. Hemse Group (*Lower Ludlovian*), Garsby; Kvinngårde; Linde; Petesviken; Sandarve; Visne Myr.

Description. Differs from *E. punctatus* in the following features. Dorsal shield less vaulted. Glabella widens more strongly anteriorly and is less convex rarely rising above

height of cheeks at back. The four pairs of lateral tubercles tend to be smaller. Fewer tubercles on glabella; tubercles conical or hemispherical. Glabellar tubercle formula: (1-0); II-1, 2; III-1, (2*), 3; iv-(0*, 1); IV-1, 2, 3; (v-0); V-1, 2, (3); VI-1, (2, 3). Basal lateral ridges more distinct. Typically with nine tubercles on false preglabellar field, one medial. Axial furrows broader, curving more strongly inwards. Fixed cheeks less convex sloping gently inwards to axial furrows; proximal tubercles smaller than others, not overhanging axial furrows. Eye lobes more slender placed farther apart. Pseudoglabellar areas of free cheeks shorter, bearing fewer tubercles, marked off from borders by fainter depressions. Rostral plate broader and shorter, subpentagonal, usually with a tubercle proximally; swollen forwardly. Central body of hypostome less convex anteriorly; median lobe broader, with less independent convexity and projecting forwards beyond anterior border; maculae less inflated. Median part of anterior border of hypostome less thickened and less flexed; anterior border furrow narrow, faint medially. Central body and tongue more coarsely granular. Usually with a tubercle, rarely a spine, on tenth thoracic ring, sometimes on seventh or on both. Spaces between pleural ribs of pygidium sometimes exceptionally broad with low, faintly granular ridges running parallel to the ribs.

Exoskeleton tends to be preserved enrolled, with hypostome in place. In this position the pygidium lies neatly against the doublures of the free cheeks, the projecting rostral plate fitting into the narrow V formed by the inner margins of the pygidial doublure (Pl. 66, fig. 1).

Remarks. Pygidia of *E. punctatus* and *E. macrourus* show so great a range of variation in convexity, length of mucro, strength of axial and interpleural furrows, size, number, and position of tubercles that specific differentiation is impossible. Whittard (1938, p. 119) has already drawn attention to the value of the hypostome and rostral plate in distinguishing species of *Encrinurus*.

The low ridges described above as running parallel to the ribs in the pygidia (Pl. 67,

EXPLANATION OF PLATE 66

- Figs. 1a-c. *Encrinurus macrourus* Schmidt. Klinteberg Group (Lower Ludlovian), Eksta, Gotland. RS Ar. 30206, $\times 3$. Enrolled dorsal shield. Dorsal, lateral, and frontal views; see Pl. 65, fig. 1.
- Figs. 2-3. *Encrinurus punctatus* (Wahlenberg). 2a, b. Slite Group (Wenlockian), Follingbo, Gotland. RS Ar. 30221, $\times 3$. Enrolled dorsal shield. Dorsal and lateral views. Fig. 3. Slite Group (Wenlockian) Eskelhem, Gotland. RS Ar. 20320, $\times 2\frac{1}{2}$. Dorsal shield. Frontal view: see Pl. 65, fig. 9.
- Figs. 4-11. *Encrinurus tuberculatus* (Buckland). 4a-c, Wenlock Shale, Malvern Tunnel, Herefordshire. OUM C318 (Grindrod Collection), $\times 4$. Cephalon. Dorsal, lateral and anterior views. 5, Wenlock Shale, Dudley, Worcestershire. BM I 2160, $\times 2$. Cephalon and thoracic segments. 6, Woolhope Shale, Malvern, Herefordshire. BU 727 (Ketley Collection), $\times 3\frac{1}{2}$. Incomplete dorsal shield. Lateral view showing impression of axial spine on tenth thoracic ring and upturned pygidial mucro. 7, Wenlock Limestone, Dudley, Worcestershire. EU A 133, $\times 2$. Cranidium with basal lateral ridges well developed; palpebral lobe strongly tuberculate. 8, Wenlock Limestone, Malvern Tunnel, Herefordshire. BM In. 42623, $\times 3\frac{1}{2}$. Specimen with three instead of the usual four tubercles in row II of the glabella. 9, Wenlock Limestone, Dudley, Worcestershire. BU 728 (Ketley Collection), $\times 2$. Pygidium. Lateral view, showing articulating facet. 10, Wenlock Shale, Malvern, Herefordshire. OUM C160 (Grindrod Collection), $\times 2$. Elongate dorsal shield. 11, Woolhope Shale, Malvern, Herefordshire. BU 729 (Ketley Collection), $\times 2$. Thorax and pygidium. Axial spine on tenth thoracic ring.



1a



1b



1c



2a



2b



3



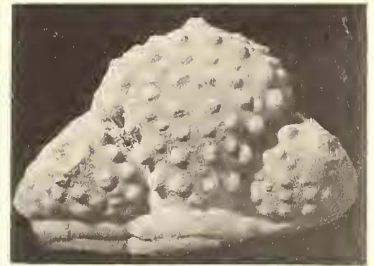
4c



5



4b



4a



6



10



7



8



9



11

fig. 3) are considered homologous with the anterior bands of pleurae in cybelid pygidia, indicating that the ribs are equivalent to the posterior bands only, not to the fused posterior band of one pleura and the anterior band of the next, the generally accepted view first promulgated by Barrande (1852, pp. 216-17).

Encrinurus stubblefieldi sp. nov.

Plate 65, fig. 12; Plate 67, figs. 14-15; Plate 68, fig. 11

Diagnosis. Cranium broad, weakly convex. Basal lateral ridges of glabella well developed; only two rows of tubercles on frontal lobe. Eight tubercles on false preglabellar field. Seven pairs of pleurae in pygidium.

Holotype. GSM 36846 (internal mould of cranium). Pl. 65, fig. 12; Pl. 67, fig. 15. 'Upper Ludlow Shales', Whitcliff, Shropshire.

Dimensions:

Median length of cranium	5.6 mm.
Width of cranium (est.)	22.5 mm.
Width across false preglabellar field	5.2 mm.
Width of glabella across basal lobes	3.2 mm.

Paratype. GSM 36844 (internal mould of cranium, thoracic segments, and pygidium). Pl. 67, fig. 14. 'Upper Ludlow Shales', N. E. Pilliard's Barn, Shropshire.

Occurrence. 'Lower Ludlow Shales'. Leintwardine, Shropshire. 'Upper Ludlow Shales', Whitcliff and N.E. Pilliard's Barn, Shropshire.

Description. Differs from *E. punctatus* in the following features. Cranium is broad and only weakly convex. Glabella widens less towards front. Glabellar tubercle formula: I-1; II-1, 2; (iii-0); III-1, 2 (*), 3; iv-(0*, 1); IV-1, 2, 3; (v-0); V-1, 2, (3). Basal lateral ridges extend to a median pair of tubercles or a single tubercle. Axial furrows broader and shallower. Cheeks broader compared with glabella. Palpebral lobes placed farther from glabella; palpebral furrows deeper and broader. Tubercles on cheeks smaller and more numerous. Fixigenal spines and adjacent borders much broader. Posterior borders finely tuberculate. Thorax narrower than cranium and narrowing more strongly towards back. Axis less than one-third anterior width of thorax. No indication of presence of axial spines. Pleural tubercles larger, situated at varying distances from axis. Pygidium shorter, composed of about eighteen rings and seven pairs of pleurae. Three or four axial tubercles, first on third ring. Pleural tubercles faint, placed fairly close to axis. Mucro slender, about half length of axis.

Remarks. No described species appears to be closely related to *E. stubblefieldi*.

Encrinurus omniensis Whittard

Plate 65, fig. 16; Plate 67, fig. 16

Encrinurus omniensis Whittard 1938, p. 118, pl. 4, figs. 6-10 (*non* fig. 11).

Diagnosis. Glabella pyriform, narrow, less elevated than cheeks at back. Eight tubercles on false preglabellar field. Eye lobes small.

Syntypes. GSM 55488 and 55489 (counterparts of an exoskeleton); OUM C1 (internal mould of a dorsal shield).

Occurrence. Purple or Hughley Shales (Upper Llandovery), Onny River Section, near Cheney Longville, Shropshire.

Remarks. The glabellar tubercle formula of the syntype OUM C1 (Pl. 65, fig. 16; Pl. 67, fig. 16) is as follows; 1-0; II-1, 2; iii-0; III-1, 2*, 3; iv-1; IV-1, 2, 3; V-VI-1, 2. A cranium from the arenaceous Purple Shales of the Bog Mine Inlier (BM In. 22533) has thirteen tubercles on the false preglabellar field, and does not belong to the species-group. Pygidia from this locality (Whittard 1938, pl. 4, fig. 11) are more triangular, more strongly vaulted and are non-mucronate.

EXPLANATION OF PLATE 67

- Figs. 1-4. *Encrinurus macrourus* Schmidt. 1, Hemse Group (Lower Ludlovian), Visne Myr, parish of Fardhem, Gotland. RS Ar. 30415, $\times 6$. Hypostome. 2, Gotland (exact locality and horizon unknown). RS Ar. 47146, $\times 8$. Left lateral view of inverted cephalon to show articulation of cranium and hypostome. Left free cheek removed, rostral plate in position; longitudinal median lobe of hypostome projects beyond anterior border. Wing process of hypostome rests against fossula near front of axial furrow; wing extends forwards close to axial furrow well beyond facial suture; posterior part of the wing is upturned, running subparallel to steeply sloping part of the axial furrow. 3, Klinteberg Group (Lower Ludlovian), Eksta, Gotland. RS Ar. 30674, $\times 6$. Pygidium. Oblique view showing ridges between ribs, considered equivalent to anterior bands of cybelids. 4a, b, Hemse Group (Lower Ludlovian), Petesviken, parish of Hablingbo, Gotland. PIT Tr 1905 (lectotype), $\times 3$. Thorax and pygidium; axial tubercles on seventh and tenth thoracic rings. Dorsal and lateral views. Photos kindly supplied by Dr. R. Männil.
- Figs. 5-8. *Encrinurus punctatus* (Wahlenberg). 5, Jaani Marl, Jaani, Saaremaa, Estonia. PIT Nr. 1922 (Luha Collection), $\times 4$. Hypostome. 6, Jaani Marl, Jaani, Saaremaa, Estonia. PIT Tr 1882. (Böläu Collection), $\times 2$. Cephalon. Oblique lateral view showing apodemal pits; see Pl. 65, fig. 14. 7, Slite Group (Wenlockian), Follingbo, Gotland. RS Ar. 47294, $\times 4$. Doublure of pygidium. 8a, b, Slite Group (Wenlockian), Vikers, parish of Boge, Gotland. RS Ar. 30223, $\times 4$. Hypostome figured by Lindström, 1901, pl. 4, figs. 5, 6, 12, 13. Plan and anterior views.
- Figs. 9-10. *Encrinurus tuberculatus* (Buckland). 9a, Wenlock Shale, Malvern, Herefordshire. BM In. 48008, $\times 3$. Hypostome. 9b, the same, $\times 2$. Ventral view of cephalon, showing underside of right axial furrow; arrow points to the facial suture, fossula lies close behind. 10, Wenlock Limestone, Malvern, Herefordshire. BM In. 48015, $\times 3$. Anterior view of inverted cephalon; rostral plate and part of left free cheek removed. Note strong median flexure of anterior border of hypostome.
- Figs. 11-13. *Encrinurus deomenos* sp. nov. 11, Jupiter Formation, The Jumpers, Anticosti Island. HM A.884, $\times 3$. Cranium. 12, Zone 4, Jupiter Formation, Sandcliff, Anticosti Island, YU 882 (holotype), $\times 8$. Anterior view of cephalon, showing free cheeks in contact and absence of rostral plate. 13, Zone 1, Jupiter Formation, East Cliff, west of Jupiter River, Anticosti Island. YU 10402, $\times 3$. Hypostome probably belonging to this species; figured by Twenhofel 1928, pl. 59, fig. 7 as *E. anticostiensis*.
- Figs. 14-15. *Encrinurus stubblefieldi* sp. nov. 14, 'Upper Ludlow Shales', N. E. Pilliards Barn, Shropshire. GSM 36844 (paratype), $\times 3$. Cranium and thorax. Internal mould. 15, 'Upper Ludlow Shales', Whitcliff, Shropshire. GSM 36846 (holotype), $\times 2$. Cranium; see Pl. 65, fig. 12. Internal mould.
- Fig. 16. *Encrinurus onniensis* Whittard. Purple Shales (Upper Valentian), Onny River Section, near Cheney Longville, Shropshire. OUM C1, $\times 2$. Dorsal shield; see Pl. 65, fig. 16. Internal mould.



1



5



8a



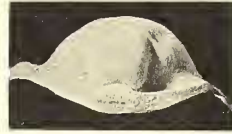
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2



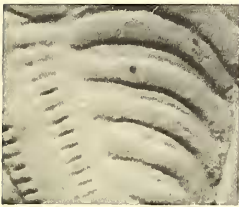
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8b



10



3



6



11



9b



13



12



4a



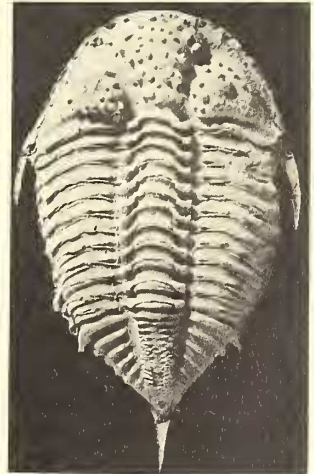
14



4b



15



16